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Notes and Records

Large herbivore dynamics in the face of insularization: the case of Lake Nakuru National Park, Kenya

The large herbivore species composition and diversity in and around Lake Nakuru National Park has changed considerably over the last century. The accounts of early travellers are replete with reports of the rich wildlife presence they encountered in the area (Eliot, 1905; Chapman, 1908; Percival, 1924, 1928; Meinertzhagen, 1957; Simon, 1962). Population sizes and movements were severely limited by the activities of early European farmers and hunters (Kutilek, 1974).

Several mammal species became locally extinct, including the Nakuru hartebeest (*Alcelaphus buselaphus cokii x jacksoni*), Masai giraffe (*Giraffa camelopardalis tippelskirchi* Matschie, 1898) and cheetah (*Acinonyx jubatus* Shreber, 1776). Others, like the white rhinoceros (*Ceratotherium simum* Burchell, 1817) and Rothschild's giraffe (*Giraffa camelopardalis rothschildi* Lydekker, 1903), are present as a result of recent introduction. More recently, areas surrounding the park were settled by a large number of mainly small-scale subsistence farmers. A high-voltage electric fence was erected in 1987 surrounding the whole park which, together with human activities on adjacent land, led to its complete insularization.

Total ground counts of large mammals have been conducted in the park periodically since 1970. As the park area has undergone several changes during the period under review, numbers for each species were converted to density to facilitate comparison over the years. The density for each species was expressed as biomass to give a common currency for expressing the ecological impact of different species.

Results

Table 1 presents biomass densities calculated from game count data from the park for the period 1970–92, and Fig. 1 presents best fit polynomial curves for population density of the six commonest species over the same period. For a mean annual rainfall of 823 mm per annum (Kutilek, 1974), herbivore biomass predicted for the park on the basis of a presumed biomass rainfall relationship was 9328.3 kg km^{-2}. Total herbivore biomass density has increased above this value twice since 1970, reaching 11221.2 and 9510.3 kg km^{-2} in 1973 and 1990, respectively, and remained below it between 1974 and 1986. Herbivore biomass was positively correlated to mean annual rainfall for periods up to 3 years, for counts carried out after 1986 when migrations were not possible. The highest correlation was over the 2 years preceding each count.

The defassa waterbuck (*Kobus ellypsiprymnus defassa* Ruppel, 1835) contributed more biomass density than any other species over all the years. The buffalo (*Syncerus caffer* Sparrmann, 1779) and Grant's gazelle (*Gazella granti* Brooke, 1872) populations showed similar patterns, with the upward trend continuing through to the most recent counts. Density remained low for the warthog (*Phacochoerus aethiopicus* Pallas, 1767), impala (*Aepyceros melampus* Lichtenstein, 1812) and zebra (*Equus burchelli* Gray, 1924) until 1978. Counts after 1986 showed a steady increase for all

Table 1. Large herbivore biomass densities (kg km^{-2}) calculated from game count data for Lake Nakuru National Park: 1970–92

	1970	1971	1972	1973	1975	1976	1978	1979	1986	1987	1988	1990	1991	1992
Defassa waterbuck	4904.0	4659.2	6178.7	6664.8	1043.0	1190.8	1446.7	1112.0	3024.0	4464.0	3989.3	4992.8	2831.2	1829.8
Buffalo	451.7	372.4	776.4	2162.9	66.4	124.1	280.1	8.6	764.6	1100.3	2400.2	1542.6	1746.2	2670.8
Hippopotamus	445.8	264.0	270.0	352.0	98.7	66.6	–	–	–	–	–	–	–	–
Bohor reedbuck	326.8	383.0	348.8	260.6	33.8	26.6	10.8	11.5	7.4	13.2	16.5	17.4	13.3	6.3
Impala	322.8	379.7	246.0	1276.8	234.8	283.1	225.1	112.8	429.2	570.0	806.0	1191.6	1029.4	694.6
Thomson's gazelle	135.6	111.7	103.9	159.0	52.2	43.9	26.3	9.8	12.7	17.3	47.7	42.0	38.1	41.9
Bushbuck	38.0	22.7	36.3	26.9	1.3	3.3	1.1	3.0	2.3	0.8	2.1	2.8	5.4	5.4
Warthog	7.9	5.6	3.2	15.8	2.8	7.8	6.6	4.8	125.1	216.4	231.3	374.0	706.1	629.8
Mountain reedbuck	5.9	5.6	8.4	45.1	3.1	6.6	0.8	0.2	–	2.2	2.5	7.3	1.9	0.7
Steinbuck	4.9	2.1	0.8	1.2	0.8	0.7	0.2	–	0.1	–	0.2	<0.1	0.4	<0.1
Dikdik	4.2	2.6	6.5	9.1	1.5	1.1	0.2	0.1	–	0.1	0.3	1.1	0.7	0.7
Duiker	2.3	0.4	1.8	0.7	0.2	0.3	0.2	–	–	–	–	0.2	–	0.1
Klipspringer	1.1	–	–	3.2	–	0.1	–	–	–	–	–	–	–	–
Eland	–	–	–	–	–	6.5	6.3	–	146.9	172.4	230.4	295.6	242.3	26.9
Rothschild's giraffe	–	–	–	–	–	–	56.3	70.5	200.3	364.5	305.3	619.1	621.8	246.4
Grant's gazelle	–	–	–	78.9	6.1	2.7	2.8	3.8	15.6	44.6	81.8	53.7	58.4	52.2
Black rhinoceros	–	–	–	115.1	9.0	–	–	–	–	106.1	12.9	33.5	5.7	17.1
Bush pig	–	–	–	–	1.4	1.0	1.0	–	–	–	2.2	3.0	0.4	0.8
Burchell's zebra	–	–	–	49.2	29.7	19.3	9.4	–	127.4	108.2	199.7	333.6	356.2	395.2
Total	6650.9	6208.9	7980.6	11221.2	1584.7	1784.4	2073.9	1336.8	4855.7	7180.0	8328.5	9510.3	7657.3	6618.8

– = species not sighted during the counts

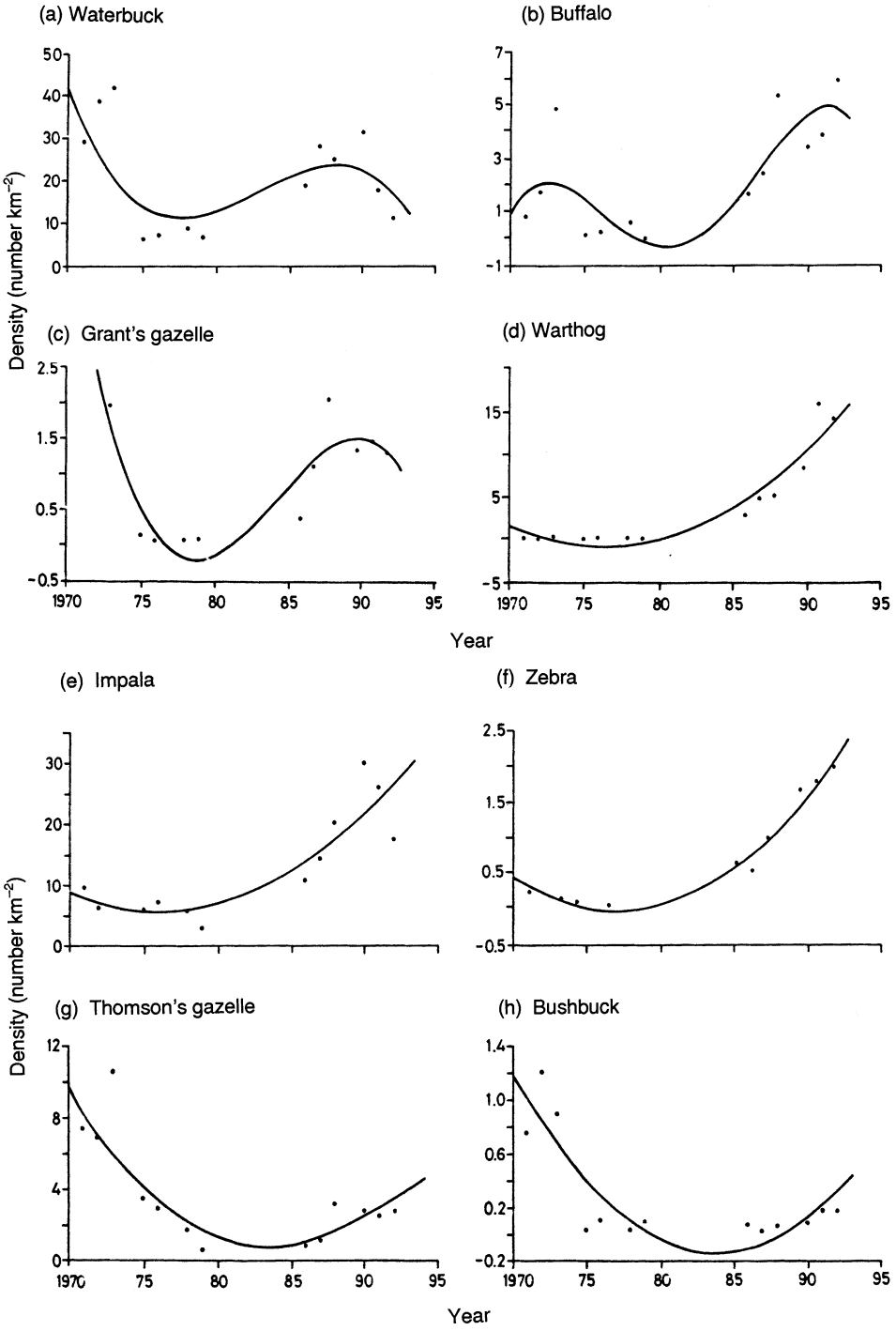

Fig. 1. Best fit polynomial curves for the density of six common herbivore species in Lake Nakuru National Park between 1970 and 1992.

the three species. The reverse was true for trends exhibited by Thomson's gazelle (*Gazella thomsoni* Gunther, 1884) and bushbuck (*Tragelaphus sylvaticus* Pallas, 1776). The Rothschild's giraffe and eland (*Taurotragus oryx* Pallas, 1766) also showed noticeable upward trends, whereas populations of the Bohor reedbuck (*Redunca redunca* Pallas, 1767) declined after 1973.

There is a direct association between annual rainfall and large African herbivore biomass (Coe, Cummings & Phillipson, 1976). Over the range of data available, a highly significant least-squares log–log regression of herbivore biomass on rainfall was found. Western (1991) analysed data from 114 ecosystems throughout Africa and concluded that total production increases with rainfall. Mixed wildlife livestock systems were more productive than protected areas, and wildlife production was lower outside protected areas as a result of competitive displacement by livestock (*op cit*.).

Large herbivore communities are known to be ultimately limited by their food supply (Sinclair, 1974; Coe *et al*., 1976; Walker, 1989; Western, 1991). This suggests that the relationship between rainfall and herbivore biomass operates through the effects of precipitation on primary production. This study suggests that, because of the ecological isolation of the park, large mammal populations can be maintained at desired equilibrium levels only through continued monitoring and active management.

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